PAPER 5

Environmental determinants of biogeography and evolution in Terra Australis

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The distribution of organisms and populations in space and in time is a complex function of the coupling of ecophysiological responses and environment. The response of an organism to its environment is the result of genetically programmed morphology and physiology (and behaviour, in animals), interacting with available environmental resources, but modified through competition and predation. The genetic program is the product of evolutionary history and, as such, can provide valuable insight into the timing and pathways of adaptation within phyletic groups. However, immense efforts devoted to the study of biological variation are not matched by equivalent efforts to analyse genotype/environment interactions and to quantify environmental parameters. Accordingly, much of the biogeographic literature rests upon simplistic and often naive assumptions about the physical environment in general and of climate in particular.

Logically, we require more complete understanding of distribution patterns under present day environment, before we can hope to understand the past. For much too long, the known climatic oscillations of the Quaternary have provided a useful catchall explanation for observed patterns of taxonomic diversity and speciation. But how much of the observed variation can be explained by differential response to present day environments? How representative are present day environments in relation to the sequences of environments through Quaternary and Tertiary time? Can we identify broad ecophysiological response groups and chart their progress through space and time? These are but some of the questions addressed in this paper.

Basic concepts and methods

At any given location the assemblage of plants and animals present is composed of organisms with different environmental requirements and sensory capacities. Each has its own *umwelt* or specific subset of relevant environmental factors. Thus, an experimental, autecological approach to the definition and measurement of specific environmental requirements seems to be indicated and necessary. But, given the enormity of the task of evaluating all taxa across all possible environmental gradients, this approach is unlikely to yield general solutions. If it were possible to categorize general classes of response to primary environmental factors then it should be possible to develop a general framework for analysis of biogeographic pattern and evolutionary process.

Analysis of causal pathways and linkages between organisms and environment suggests that a functional grouping of environmental variables in terms of the major dynamic regimes that modulate plant and animal response (light, thermal, water, nutrient, biotic) is likely to be most useful in developing a general framework (Nix 1978). In what follows a further generalization assumes the primacy of plant/environment interactions, i.e. animal distribution patterns are some function, albeit complex, of primary plant productivity and resultant vegetation structure. A more complete understanding of plant/environment interactions is seen as an essential prerequisite for any analysis of animal distributions.

The basic methodology adopted involves the coupling of generalized models of plant response to an extensive climatic data base for the region studied, i.e. the Australia-New Guinea region, hereafter identified as Terra Australis (Nix 1981a). Purpose and scale remain vital considerations in any such application. A central problem is to maintain an appropriate balance between model development and the inherent limitations of the environmental data base. More precise specification of both ecophysiological responses and of the physical environment may be necessary for autecological studies, but increasing precision leads to decreasing generality. Thus, simplifying assumptions and normalized response functions become necessary for a macroscale, synecological study. Provided that these be explicit, all results are amenable to checking and to comparative analysis using different assumptions and response functions.

The plant response model

The model used here is labelled GROWEST (= GROWth ESTimation) and represents a further development and elaboration of that originally developed by Fitzpatrick and Nix (1970) for use in a comparative analysis of temperate and tropical pasture species in Australia. Very briefly, the model comprises a set of functions that transform the dynamic, non-linear responses of plants to the major environmental regimes into dimensionless indices on a linear scale of zero to unity. The core functions are capable of simple adjustment and manipulation to represent a wide range of potential variation in plant response to environment. The general concept has proved to be remarkably robust and useful in a very wide range of applications (e.g. Nix & Kalma 1972; Nix & Austin 1973; Nix 1976; Austin & Nix 1978) and as a basis for further development of generalized plant response models (e.g. Specht & Brouwer 1975; Medd & Smith 1978; Angus *et al.* 1980).

The core functions in the model that relate plant response to the major climatic regimes of radiation, temperature and water are shown in Figure 1. Each of the derived environmental indices, light index (L.I.), thermal index (T.I.), and water or moisture index (M.I.), represents dry matter production relative to dry matter production at non-limiting values of that factor. Thus, each index has values ranging from zero (completely limiting conditions) to unity (non-limiting conditions). In addition, separate indices may be derived for response to soil fertility gradients and for specific biotic constraints such as competing species.

Light response functions

The response of plant canopies to light energy is a complex function of plant population, stand geometry, canopy cover, physiological properties and the photosynthetically active component of solar radiation. However, at the level of generalization adopted here, the range of possible normalized responses is represented by a set of exponential functions. Broad limits are set by the envelope between the inner and outer curves shown in Figure 1a. The outer curve would typify a shade-tolerant type of response and the inner curve a shade-intolerant response. An intermediate curve is used in the present analysis and has the form,

$$\text{L.I.} = 1.0 - e^{-3.5x}$$

where L.I. = light index

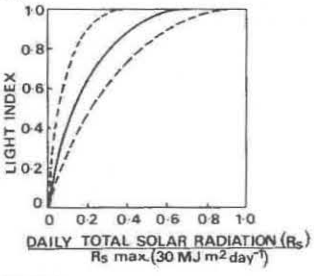
x = daily total solar radiation/30 MJ m^{-2} day^{-1}

While a given function may be used for comparative geographic analysis of response for a specified plant group, it must be stressed that absolute values of dry matter response differ significantly between groups. Thus, for instance, C_4 grasses may have maximum daily growth rates of 40-60kg $ha^{-1}day^{-1}$ compared with C_3 plants generally that may attain maxima of only 20-30kg $ha^{-1}day^{-1}$.

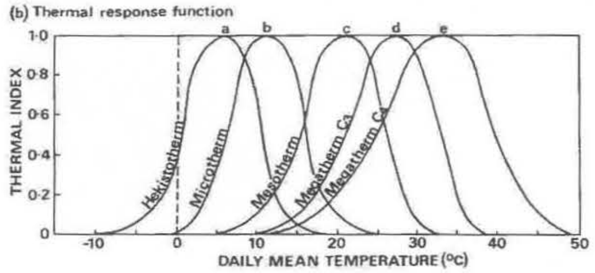
Temperature response functions

Plant species exhibit characteristic response curves to temperature with a lower and an upper temperature threshold for growth and an intermediate optimum. Beyond the upper and lower temperature limits for growth there are lethal limits. Using controlled environment facilities it is relatively simple to establish a response curve for a target species, but it is essential that adequate light energy be available for high temperature treatments or the form of the response will be distorted. In deriving the thermal response functions shown in Figure 1b the total above-ground dry matter increment during a specified time interval (preferably during vegetative growth) was used. Instantaneous measures of net photosynthesis of single leaves or of partial canopies in relation to temperature are not an appropriate measure of whole plant response.

(a) Light response function



(b) Thermal response function



(c) Moisture response function

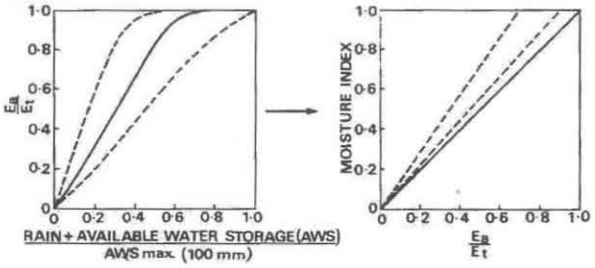


Fig. 1. Core functions used in GROWEST (GROWth ESTimation) model: **a**, light response function; **b**, thermal response function; **c**, moisture response function.

When considering the whole range of thermal environments and the entire plant kingdom it seems reasonable to expect a continuum of plant response to temperature. This may, ultimately, prove to be so, but analysis of existing data suggests that a limited number of distinctive plant groups can be recognized, each exhibiting broadly similar thermal responses. Five such groups are recognized here, although further subdivision may be warranted when response data become available. The terminology adopted follows that of de Candolle (1855), who recognized broad groups but offered no quantitative definitions. Also, there is a subdivision of one group based on dominant photosynthetic differences.

MEGATHERM (A) C_4 and CAM photosynthesis: optimum 30-33°C; lower threshold 10°C; upper threshold 46°C.

MEGATHERM (B) C_3 photosynthesis: optimum 26-28°C; lower threshold 10°C; upper threshold 38°C.

MESOTHERM C_3 photosynthesis: optimum 19-22°C; lower threshold 5°C; upper threshold 33°C.

MICROTHERM C_3 photosynthesis: optimum 10-14°C; lower threshold 0°C; upper threshold 25°C.

HEKISTOTHERM C_3 photosynthesis: optimum 6-8°C; lower threshold -10°C; upper threshold 20°C.

The derived curves shown in Figure 1b are specified mathematically by a combination of power functions based upon the relative temperature deviations above or below the specified optimum temperature (Nix 1981b). The thermal response functions so derived are merely representative of broad plant groups. Individual taxa within any of these broad groups may show deviations of 2-3°C about any of the stated values, but rarely more. However, very significant differences between taxa within broad response groups do occur with respect to lethal temperature limits. These limits will determine the ultimate survival of an organism in a particular location, but the broad growth response will determine vigour, growth pattern and competitive ability.

The recognition of defined thermal response groups is deliberate and obviates the confusion in the literature associated with the use of 'tropical', 'sub-tropical' and 'temperate', terms that have geographic as well as thermal connotations. For example, optimum thermal environments exist along an elevational gradient within the tropics for all five groups. Many taxa that are designated 'tropical' because of present day distribution patterns are, in reality, mesotherm or even microtherm elements. The very high taxonomic diversities recorded for many tropical countries are due to the presence of high mountains that provide near-optimal thermal environments for all major response categories, particularly where this is combined with near-optimal moisture, light and nutrient regimes.

Water response functions

The moisture index (M.I.) is calculated using a simple water-balance that requires as input only precipitation and potential evaporation data. Tuning of the water-balance model to fit a specified set of vegetative cover, soil and climatic conditions is achieved by the following.

(a) Adjusting the relationship between potential evapotranspiration (E_t) and potential evaporation (E_o) as a function of canopy cover. E_t/E_o can be made a function of canopy development and canopy senescence rates in annual plants or it can be fixed at an appropriate level for stable canopy cover achieved by perennial communities (*cf.* Specht 1972). With full canopy cover, $E_t/E_o = 1$.

(b) Adjusting the maximum extractable water in the root zone (100mm is a commonly used reference level, but shallow sands may have less than 25mm and deep, structured loams more than 300mm).

(c) Adjusting the form of the drying curve, or the ratio of actual evapotranspiration (E_a) and potential evapotranspiration (E_t) as a function of relative extractable water in the root zone. Continuous functions of exponential form are used to represent different soil textural classes, as shown in the first function in Figure 1c.

(d) Adjusting the form of the relative dry matter response to increasing water deficit as indicated by E_a/E_t and shown in the second function in Figure 1c. The general form is taken to be a linear reduction, but with differing initial thresholds before onset of water-stress reduction in growth. Thus, mesic taxa show an immediate reduction in growth response with decline in E_a/E_t, while xeric taxa may show no reduction until E_a/E_t falls below 0.9 or even 0.8. In the latter case, specialized features decouple to some extent the normally closely related processes of transpiration and CO_2 uptake in photosynthesis.

In the present study the functions used are shown as solid lines in Figure 1c. For comparative analysis it has been assumed that the vegetation at any given location can achieve full canopy cover (i.e. $E_t/E_o = 1.0$) when the water regime is non-limiting, and that the maximum extractable water in the root zone is 100mm. Although conceptually simple, the water-balance model is capable of considerable refinement and elaboration to cater for specific situations.

The multifactor growth index

Separate indices are combined, finally, in a single multifactor growth index (G.I.). Obviously no single, simple relation can adequately describe complex genotype/environment interactions. But, for simplicity, the choice lies between the classical Liebig's law of the minimum (the value of the most limiting factor becomes the value of the growth index), averaging, or a multiplicative index. Sensitivity analysis indicates that there is little to choose between these three alternatives, but that the multiplicative index is marginally superior. In the present study then,

$$G.I. = L.I. \times T.I. \times M.I.$$

Thus, the multifactor growth index (G.I.) has values ranging from zero to unity and can never exceed the value of the single most limiting factor.

The climatic data base

Development of a matching data base must proceed in parallel with model development. For broad-scale spatial analysis an extensive network of stations is desirable. The very limited network available for measurement of key climatic elements such as solar radiation and potential evaporation means that additional effort is required in development and testing of estimation procedures. Continuing additions and improvements have been made to operational climatic data files, that are accessed on magnetic tapes labelled AUSCLIMEANWK and NGCLIMEANWK. Long-term weekly mean data have been derived from climatic normals of monthly means by interpolation procedures for some 800 stations in Australia and 77 stations in New Guinea. For each station is listed: name; latitude; longitude; elevation (m); photoperiod (hrs); total daily solar radiation (MJ $m^{-2}day^{-1}$); maximum temperature (°C); minimum temperature (°C); day mean temperature (°C); night mean temperature (°C); 24 hour mean temperature (°C); vapour pressure (mb); relative humidity (%); precipitation (mm); class 'A' pan evaporation (mm); Penman potential evaporation (mm); Priestley-Taylor potential evaporation (mm).

In the present study, climatic data inputs required for the environmental analysis of Terra Australis are limited to total daily solar radiation, mean temperature (24 hour), precipitation and Penman potential evaporation.

Environmental analysis

The concentric zonation of rainfall in 'dry' continental Australia and the contrast with 'wet' New Guinea focuses attention on the water regime as a major determinant of biogeographic pattern and evolutionary process. But the thermal regime is no less significant. Four thermal response groups are of areal significance in the flora of Terra Australis under present climate. Since one of these groups, megatherm C_4, commonly forms a grass ground-storey under perennial trees and shrubs of another group, megatherm C_3, and since both have broadly parallel distribution patterns, only the latter group is considered here. Thus, for simplicity, three broad thermal response groups, all C_3 photosynthetic pathways, form the basis of this analysis, namely the megatherm, mesotherm and microtherm groups.

For each of these primary groups separate values of the light, thermal, moisture and multifactor growth indices were calculated for each week using climatic data from some 900 locations in Terra Australis. These data in turn provided the basis for calculation of selected measures of environment as determined by basic plant response. Included are annual and seasonal means, standard deviations, coefficients of variation and running quarterly (13 week) means. The last provide a useful measure of the timing and value of the most favourable and least favourable seasons.

Light regimes

The latitudinal position of Terra Australis ensures potentially high input of daily total solar radiation throughout the year. Indeed, for most of Australia and much of lowland New Guinea mean daily solar radiation exceeds 16 MJ m^{-2}day^{-1}, at which level the light index (L.I.) exceeds 0.8. However, the central cordillera of New Guinea shares with the west coast of Tasmania the distinction of having the lowest mean daily solar radiation values of less than 12 MJ m^{-2}day^{-1}. In contrast, the arid inland core of continental Australia has values ranging upwards from 20 MJ m^{-2}day^{-1} to beyond 24 MJ m^{-2}day^{-1}. Thus, one very distinctive feature of the Australian arid environment is a high mean daily solar radiation input.

In general, the light regime is rarely the major limiting factor. Although solar radiation levels are substantially reduced in winter in southern Australia, due both to the sun's position and attenuation by cloud, plant productivity is limited even more by low temperatures. A singular exception to this generalization is New Guinea, where water and thermal regimes may be near optimal, but light regime moderately limiting. However, light index values seldom fall below 0.7 even in the highest rainfall and/or cloudiest environments and/or seasons.

More subtle effects of the radiation regime follow from differential responses of plants to increasing radiation (*cf.* Fig. 1a). Shade-tolerant taxa become competitive at lower light levels. Although fluctuations in the areal extent and dominance of ancient plant groups such as *Nothofagus* and the austral conifers are usually attributed to shifts in temperature and water regime, I think it is likely that shifts in the light regime have been of equal if not greater importance. In reducing radiation, continuous cloud cover leads to shifts in the carbon balance (as simply measured by a photothermal quotient, P.T.Q., measured in units of MJ m^{-2}degree-day^{-1}); this confers advantages on plant taxa with a lower temperature threshold for development. This may be one reason for the observed occurrence of cooler-adapted floristic elements at lower elevations in continuously cloudy environments in the tropics and for the persistence of austral conifers such as *Araucaria* in cloudy scarp zones along the northeastern coast of Australia.

Thermal regimes

The pattern of plant thermal regimes mirrors latitudinal and altitudinal temperature gradients within Terra Australis (Fig. 2). A thermal response group has been classed as dominant only when its annual mean thermal index (T.I.) value exceeds 1.25 times that of adjacent response groups. This allows for mesoscale variations in temperature and for differences in ecophysiological adaptation within response groups, and emphasizes the point that broad interzones rather than sharp boundaries must be expected. The broadscale patterns of dominant zones and interzones shown in Figure 2 relate to temperature environment only.

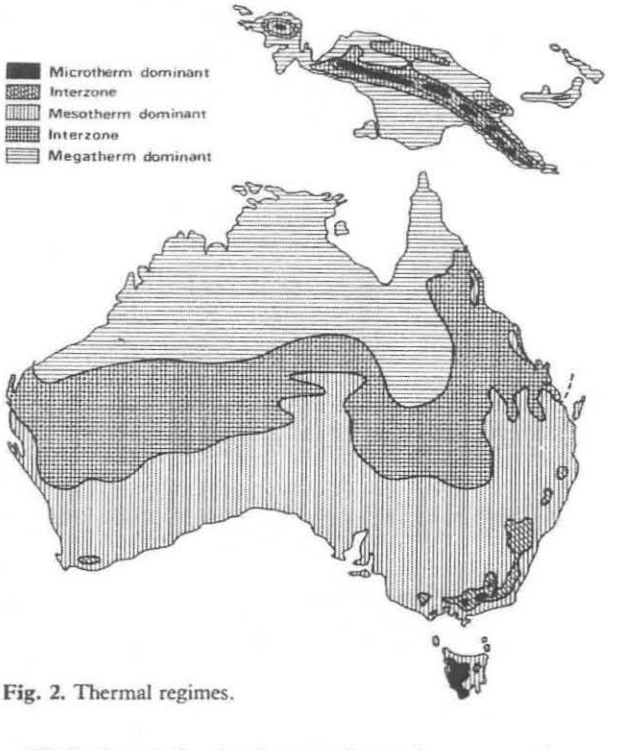


Fig. 2. Thermal regimes.

While the relative dominance of megatherm, mesotherm and microtherm elements is illustrated in Figure 2, there is a decline in absolute thermal index (T.I.) values for all three groups with increasing latitude. Increasing seasonality of temperature regime with latitude is tempered to some extent in coastal, insular and maritime regions. Optimal thermal environments for each of the megatherm, mesotherm and microtherm elements are found within New Guinea where successive replacement with increasing elevation is shown in Figure 3. Since moisture and light regimes also tend to be near optimal, this emphasizes the fact that optimum growth conditions for each of the three groups occur today in New Guinea. The very high taxonomic diversity reported for many tropical regions owes much to this vertical stacking of near-optimal environments for discrete thermal-response elements.

In very broad terms, the megatherm element is dominant where mean air temperature exceeds 24°C, a megatherm/mesotherm interzone is indicated where mean air temperatures are less than 24°C and greater than 20°C, the mesotherm element is dominant where mean air temperatures fall between 14°C and 20°C, a mesotherm/microtherm interzone is indicated where mean air temperatures are less than 14°C but greater than 12°C, and the microtherm element is dominant where mean air temperatures fall below 12°C.

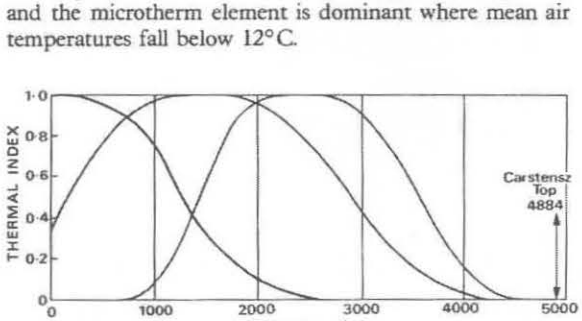


Fig. 3. Relative response of megatherm, mesotherm and microtherm groups with elevation in New Guinea.

The influence of the eastern highlands of Australia and the central cordillera of New Guinea in distorting otherwise broadly latitudinal zonation of thermal regimes is evident in Figure 2. Within the arid zone of Australia the influence of the central highlands and mountain ranges on northward extension of mesotherm environments is clearly shown, as is the influence of the eastern lowlands in extending the megatherm environment southwards. Those familiar with plant and animal distributions in arid Australia will recognize patterns that closely match those shown in Figure 2.

Within the arid zone of Australia there is an almost equal division between a northern, megatherm-dominant zone, a southern, mesotherm-dominant zone and an intermediate zone of overlap where both elements occur. The megatherm element is characterized by prominence of phyllodinous acacias, tiliaceous shrubs and the grasses *Triodia* and *Aristida*. In turn, the mesotherm element is characterized by prominence of malvaceous shrubs, Chenopodiaceae and the grass *Stipa*. The southward extension of the megatherm element in the overlap zone is characterized by the occurrence of tree species such as *Eucalyptus dichromophloia* and *E. terminalis, Brachychiton gregorii, Lisiphyllum gilvum, Grevillea striata, Owenia acidula* and *Erythrina vespertilio.*

When the influence of the water regime is added to that of the thermal regime there are some important adjustments to the patterns shown in Figure 2. Obviously, the timing of water availability in relation to prevailing temperature will influence resultant patterns. Very briefly, the megatherm element expands at the expense of the megatherm/mesotherm overlap because of the coincidence of seasonal rainfall with high summer temperatures. In Tasmania and southern Australia, the microtherm element and microtherm/mesotherm overlap expand at the expense of the mesotherm element because of the coincidence of seasonal rainfall and lower winter temperatures. The integrated influence of light, thermal and water regimes on each of the major groups is considered later.

Water regime

Patterns of annual mean precipitation are quite sufficient to demonstrate the sharp contrast between predominantly arid, continental Australia and predominantly humid, insular New Guinea. Most of New Guinea has annual mean precipitation exceeding 2000mm, while less than one third of Australia has values exceeding 500mm and another third, the arid continental core, has values less than 250mm. However, this arid core region of Australia has significantly higher mean rainfall than is recorded for other mid-latitude deserts such as the Sahara and the Kalahari. Although frequently cited, annual mean precipitation patterns have limited value for all but the broadest and simplest forms of biogeographic analysis.

Seasonality of precipitation exerts a major influence on biogeographic patterns and modes of adaptation. Basic patterns of rainfall seasonality in Terra Australis have been analysed by Fitzpatrick (1964) for Australia, and by Fitzpatrick *et al.* (1966) for New Guinea. Across southern Australia the pattern is one of wet winter/dry summer, while across northern Australia and in a small segment of southern New Guinea this pattern is reversed, i.e. wet summer/dry winter. Much of New Guinea and eastern Australia has rainfall in both summer and winter. To take account of relatively high year-to-year variability in seasonal rainfall, Nix (1981a) shows patterns of summer (November-April) and winter (May-October) seasonal rainfall equalled or exceeded in eight years out of 10 in Terra Australis. At this level of probability, a high proportion of the area of continental Australia receives less than 100mm of rainfall in either season.

While providing some useful generalizations, these rainfall-based descriptors of water regime do not provide an adequate measure of plant response to water supply and evaporative demand. The water-balance approach is indicated, and that used in this study has been described earlier. Although conceptually simple, this takes account of vegetative cover, the buffering effects of soil water storage and losses from the system. The measure of plant response to water regime, the moisture index (M.I.) used here, is linearly related to the ratio of estimated actual to potential evapotranspiration (E_a/E_t).

Two separate measures are employed to highlight the more significant features of the water regimes in Terra Australis. Firstly, using a threshold concept, the number of weeks per year in which the moisture index is less than 0.25 has been calculated and mapped (Fig. 4). At M.I. values less than this threshold (0.25) plant response is severely limited by water stress. For simplicity, the 0, 13, 26, 39 and 52 week isolines are plotted, as these separate quarter-year (13 week) periods. The patterns in Figure 4 highlight the differences between New Guinea and Australia. Much of New Guinea, but only very limited and disjunct enclaves in eastern Australia, plus a larger area in southwest Tasmania have zero weeks of water stress. In these environments, closed canopy formations are dominant and range from tall forest to low heath and sedgeland depending on terrain and edaphic controls.

A significant part of southeastern Australia and smaller sectors in Tasmania, southwestern Western Australia and southern New Guinea have less than one quarterly period (13 weeks) of water stress. Occurrence of water stress favours development of open canopies and scleromorphic

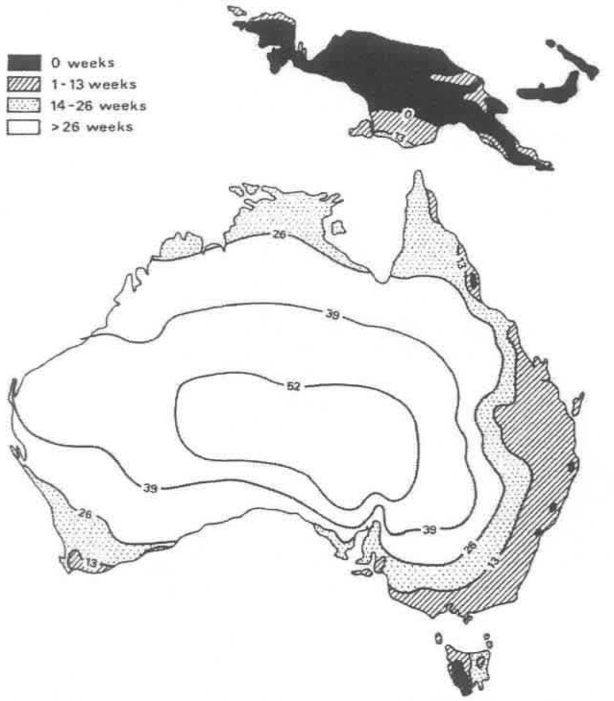


Fig. 4. Number of weeks with moisture index (M.I.) < 0.25.

attributes, and myrtaceous tree genera are prominent, e.g. *Eucalyptus, Tristania, Syncarpia, Melaleuca*. At mesoscale, protected sites and ones supplied with groundwater may carry closed canopy communites. Practically all the protected and managed forests of Australia are concentrated within this zone. Exceptions to this generalization are *Eucalyptus* open forest communities in the Cape York, Northern Territory and Kimberley regions and the jarrah (*Eucalyptus marginata*) forests of the southwest. In these cases, storage of soil-water in deep earths and gravels modifies the severity and duration of the seasonal stress period.

Woodland formations dominated by *Eucalyptus* species are best developed within the broad concentric zone that has between one quarter and one half year of water stress (i.e. 13-26 weeks <0.25 M.I.). In the next concentric zone one-half to three-quarters of each year have water stress (26-39 weeks <0.25 M.I.). Low open woodlands dominated by *Eucalyptus* species are present throughout, but most prominent in the north and east except on heavy clay soils where open tussock grasslands (*Astrebla*) are dominant. Across southern Australia, open scrublands of mallee (*Eucalyptus* spp.) are best developed in this zone.

The arid zone as usually defined by other criteria encompasses the remaining two zones. The outer concentric zone has, on average, some weeks each year without severe water stress (i.e. >39 but < 52 weeks of M.I. <0.25). Tall shrubland, dominated by mulga (*Acacia aneura*), is a prominent structural formation on deeper well-drained soils, while hummock grassland (*Triodia, Plectrachne*) is extensive on shallower, rocky and sandy soils. In the inner, arid core all weeks each year, on average, have M.I. <0.25. Vegetation formations of the surrounding zone extend into this arid core, but on heavier, clay soils chenopod low shrublands (*Atriplex, Maireana, Halosarcia*) are extensive. Sand dune systems and sandplains have mixed communities, but hummock grasslands (*Zygochloa, Triodia, Plectrachne*) are prominent.

The second measure of water regimes in Terra Australis that is used here is an index of seasonality. While various indices have been computed, that most useful for present purposes is the coefficient of variation of weekly mean moixture index (standard deviation as a percentage of mean). The patterns shown in Figure 5 again illustrate the marked contrast between New Guinea, which has mostly aseasonal water regimes, and Australia where they are mainly seasonal. The line of balance between summer (November-April) and winter (May-October) water regimes broadly bisects continental Australia and lies considerably northwards of the line of equal summer/winter rainfall that has been used by phytogeographers (*cf*. Burbidge 1960).

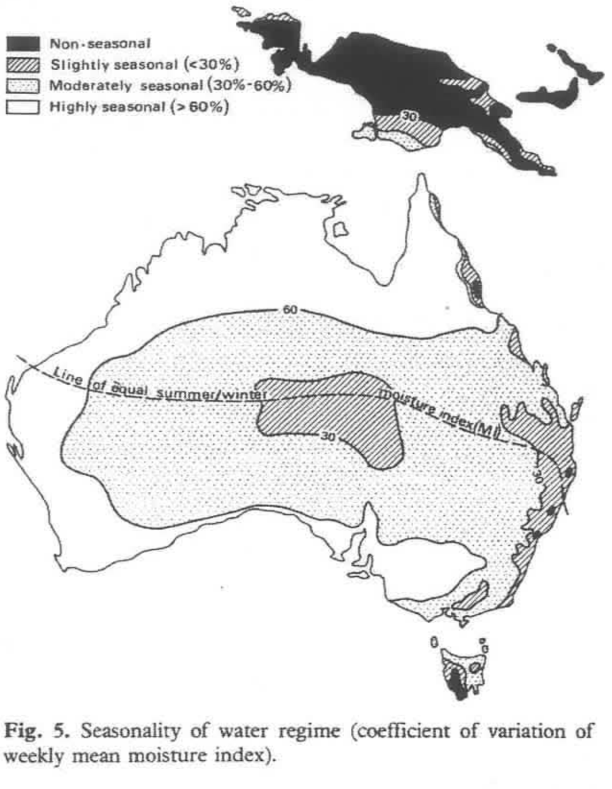

Non-seasonal
Slightly seasonal (<30%)
Moderately seasonal (30%-60%)
Highly seasonal (>60%)
30
60
Line of equal summer/winter moisture index (M.I.)
30
30
0

Fig. 5. Seasonality of water regime (coefficient of variation of weekly mean moisture index).

A broad zone of slight (<30%) to moderate (30-60%) seasonality occupies the middle section of continental Australia. Consequently, although arid (>39 weeks with M.I. <0.25 as in Fig. 4), the interior has a low probability of soil water recharge in both summer and winter seasons. This characteristic is probably of great significance for many plant and animal distribution patterns. Nix and Austin (1973) showed that mulga (*Acacia aneura*) is essentially confined within ±75 percentage deviation of seasonal moisture index from the line of balance. This corresponds closely to the 60% seasonality index boundary. Further to the east, with improving water regimes, mulga is replaced by other *Acacia* species such as gidgee (*A. cambagei*) and brigalow (*A. harpophylla*) that grade from open woodland to open forest on deep cracking clay soils.

Zones of high seasonality of water regime occur across northern Australia and extend to small outliers in southern New Guinea with a so-called 'monsoonal' climate (humid summers/arid winters). They also extend across southern Australia with its so-called 'Mediterranean' climate (humid winters/arid summers). Alternation of wet, often very wet, and dry, often very dry, seasons imposes severe constraints on the biota and calls for specialized adaptations. Zones of low seasonality (<30%) extend from Tasmania through eastern Australia to New Guinea. Within this zone continuously favourable, aseasonal water regimes occur in small disjunct areas in Australia, larger areas of southwestern Tasmania and over much of New Guinea. Older endemic elements of the biota, including those regarded as having primitive characteristics, are concentrated in such environments. This aspect is considered in more detail in a later section of this paper.

Growth regimes

While examination of the separate influences of the primary light, thermal and water regimes does provide useful insights, the integration of these separate components into a single multifactor growth index (G.I.) is likely to be most relevant. The gradients in growth response shown for each of the megatherm, mesotherm and microtherm elements have been generated solely by coupling basic ecophysiological responses to an extensive set of climatic data, as has been described earlier.

Megatherm patterns

As might be expected, most favourable environments (G.I. >0.6) for this response group are found primarily in lowland New Guinea but there are two very small lowland enclaves in northeastern Australia (Fig. 6). Closed canopy forests are dominant throughout, but are best developed in lowland New Guinea where growth conditions are close to optimal, with G.I. values approaching and exceeding 0.9. Reductions in G.I. values across northern Australia are primarily due to water limitations in the dry season, while the attenuation down the east coast is primarily due to lower winter temperatures. These differences tend to produce differential segregation of basic megatherm biota. Those adapted to seasonal water stress, but not to lower temperatures, are dominant across northern Australia, while those with a wider tolerance for lower temperatures, but intolerant of water stress, persist in a narrow strip down the entire east coast of Australia. Increasing competition from better adapted mesotherm elements is an added limitation in the south as it is with increasing elevation in New Guinea.

Biogeographers will instantly recognize a host of plant and animal distribution patterns that conform with the gradients shown in Figure 6. The continental Australian component has long been designated the Torresian biogeographic province (Spencer 1896) and the constituent biota, the Torresian element. Schodde and Calaby (1972) identify an Irian province in lowland New Guinea, with small outliers on Cape York, on the basis of vertebrate faunas. The division between Torresian and Papuasian elements broadly corresponds with megatherm mean weekly growth index values of 0.6. This approximates the boundary between mesic closed-canopy forests and more xeric open-canopy forests and woodlands. The marginal overlap of these two bioclimates in New Guinea and northern Australia is evident and is of great significance when considering biotic disjunctions between the two land masses.

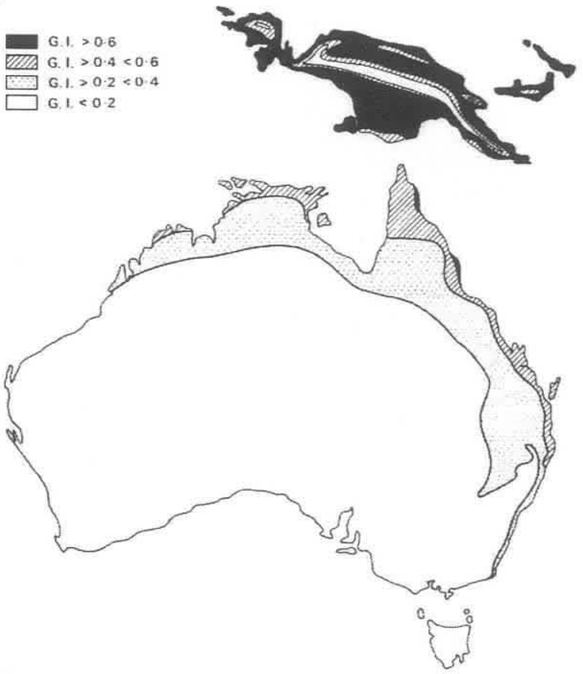


Fig. 6. Megatherm-C$_3$ weekly mean growth index (G.I.).

Mesotherm patterns

Most favourable environments (G.I. >0.6) for this response group are found at elevations of between 1000m and 2000m in New Guinea and in lowland southeastern Australia and on isolated mountains and plateaux with increasing elevation northwards in northeastern Australia (Fig. 7). Closed canopy forests are best developed in New Guinea where growth conditions are close to optimal with G.I. values approaching and exceeding 0.9, but also occur on more fertile soils down the east coast of Australia where G.I. values exceed 0.6. The best development of *Eucalyptus*-dominated open forest occurs in the zone with mesotherm G.I. values >0.4 and <0.6. *Eucalyptus*-dominated woodland and open scrub (mallee) are prominent in the zone where mesotherm G.I. values >0.2 and <0.4, with the exception of northeastern Australia and lowland New Guinea, where the environment is much more favourable for the megatherm element (*cf.* Fig. 6).

Again, biogeographers will immediately recognize plant and animal distribution patterns that conform with gradients in Figure 7. The southern half of the continental pattern broadly conforms with the classical Bassian biogeographic province of Spencer (1896). This analysis, however, suggests that Bassian or mesotherm elements will be found at increasing elevation on disjunct uplands far into north Queensland and with even greater disjunction, in the sub-montane cordillera of New Guinea. Schodde and Calaby (1972), on the basis of vertebrate faunal affinities,

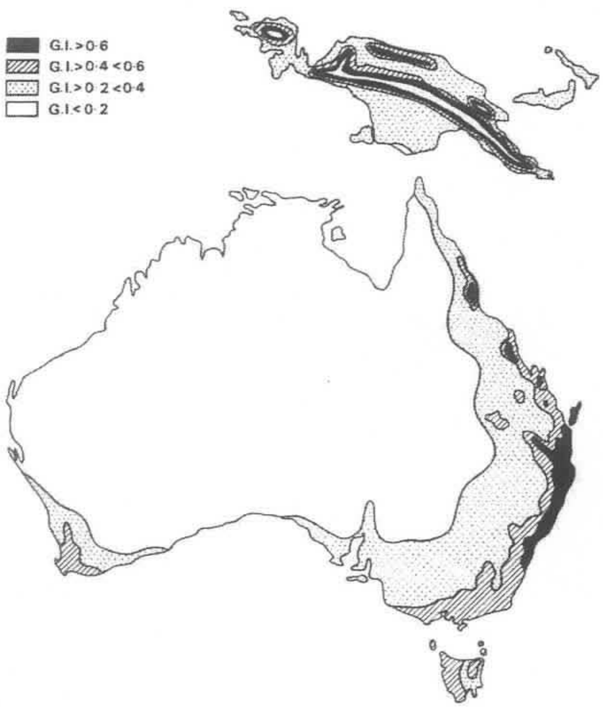


Fig. 7. Mesotherm weekly mean growth index (G.I.).

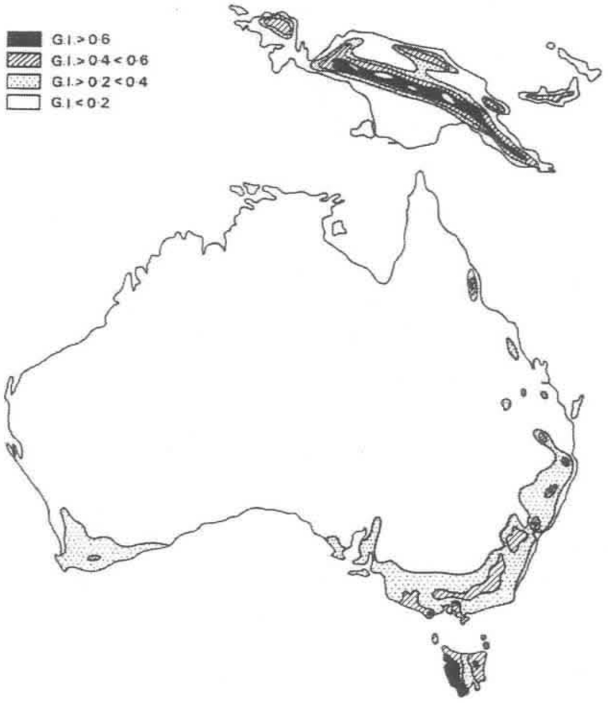


Fig. 8. Microtherm weekly mean growth index (G.I.).

identify a Tumbunan province for the montane biota above about 1200m in New Guinea and with disjunct outliers in the uplands of eastern Australia. This broadly corresponds with those environments with mesotherm G.I. values >0.6, which approximates the boundary between mesic closed-canopy forests and more xeric open-canopy forest and woodland.

Microtherm patterns

Most favourable environments (G.I. >0.6) for this response group are found at elevations of between 2000m and 3000m in New Guinea, in southwestern Tasmania and in very small, disjunct occurrences on mountains and ranges in northeast Tasmania, the Otway Ranges and mountains northeast of Melbourne in Victoria, Barrington Tops and higher points along the edge of the New England scarp in New South Wales, and higher points on the Lamington Plateau of southeast Queensland (Fig. 8). Estimated climatic data for the summit regions of Mt Bartle Frere (1622m) and Mt Bellenden Ker (1593m) in northeastern Queensland place them in this category of favourable microtherm environments. The presence of species such as *Rhododendron lochae* and *Dracophyllum sayeri* supports this assessment.

Where sufficiently large areas of favourable microtherm environment persist (montane New Guinea, southwest Tasmania) these are characterized by closed canopy forest of southern beech (*Nothofagus* spp.) and austral conifers such as *Dacrydium*, *Phyllocladus* and *Podocarpus*. Not all members of the southern beech and austral conifer groups are microtherm. *Nothofagus* species of the *brassii* type (formerly present in Australia, but now confined to New Guinea and New Caledonia) and the conifers *Araucaria*, *Agathis* and *Callitris* as well as some sections of *Podocarpus* are basically mesotherm in response.

Unlike the megatherm and mesotherm elements that span the entire range of water regimes present in Terra Australis, the microtherm element is essentially confined to environments with favourable water regimes. Arid or seasonally arid environments with temperatures favouring the microtherm element are virtually absent under present climatic regimes, but this was not always so. At times of full glacial temperature depression, there is ample evidence for the existence of cold dry climates across southern Australia (Bowler *et al.* 1976). But where are these xeric microtherm elements today? Probably they include herbs and grasses that persist in very localized, edaphically arid sites in southwest Tasmania and on higher mountains of southeastern Australia. *Stipa*, a widespread grass genus in southern Australia and Tasmania, is prominent in the xeric microtherm environments of Patagonia today (R. Galloway, personal communication). Also, analysis of growth index data based on optimum quarterly (13 week) or half-yearly (26 week) values suggests that even though mesotherm elements should predominate in the perennial, tree and shrub stratum, microtherm elements should be prominent as annuals in the ground stratum of the winter-rainfall zones of southern Australia.

Biogeographic patterns and taxonomic diversity

Dissatisfaction with the static concept of biogeographic regions has in no way hampered its continued use. The classical tripartite division of Australia into Torresian, Bassian and Eyrean zones by Spencer (1896) remains in active service. Belated recognition of New Guinea as an integral component of the evolving land mass of Terra Australis has led to further elaboration and embellishment. Hence Schodde and Calaby (1972) added Tumbunan and Irian zones in New Guinea and northeastern Australia.

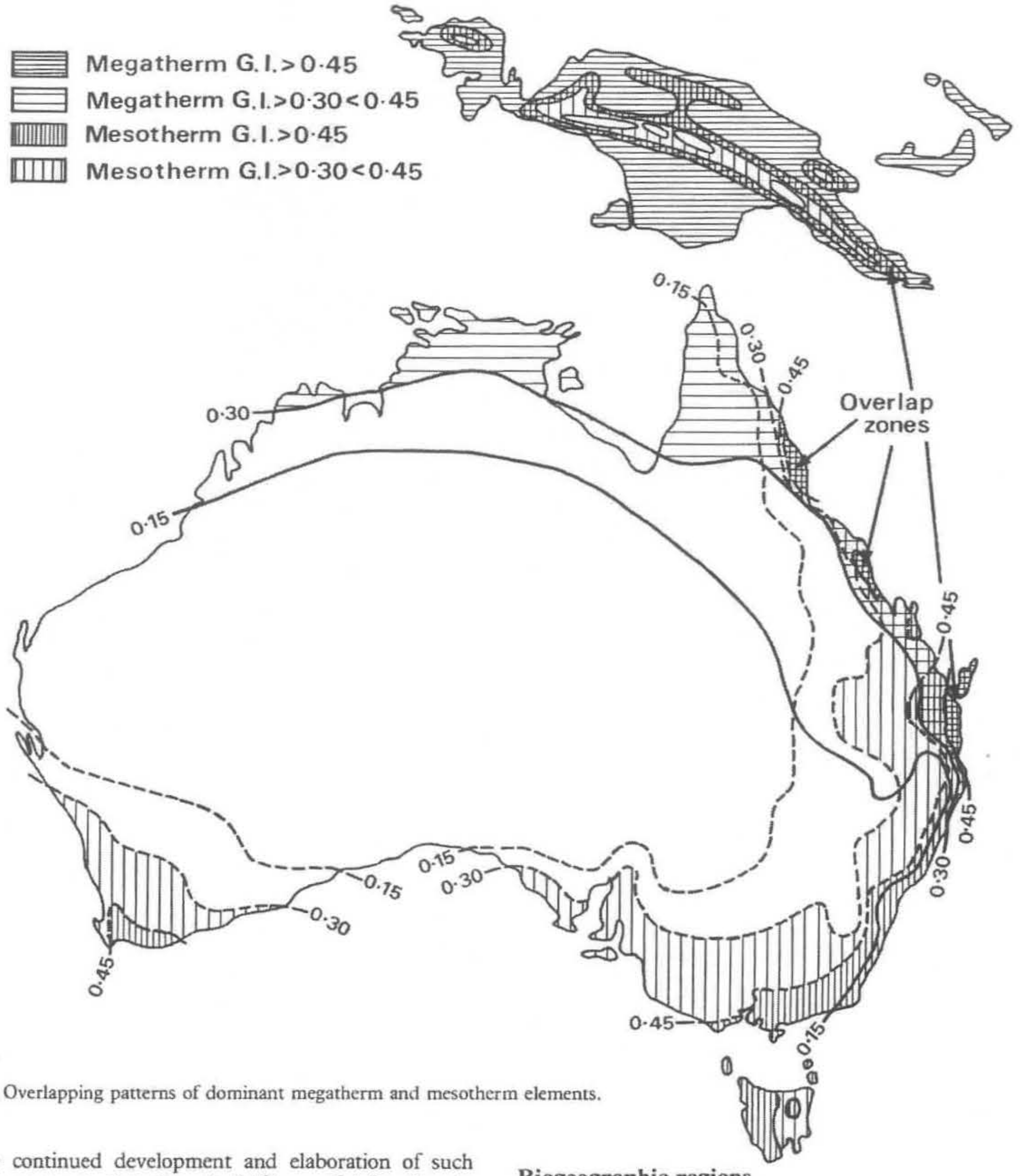


Fig. 9. Overlapping patterns of dominant megatherm and mesotherm elements.

The continued development and elaboration of such schemes suggests that they do fulfil a useful function in simplifying and communicating information about general patterns of plant and animal distribution. That such patterns can be recognized among widely disparate taxa implies that there are very powerful underlying environmental controls. The primary objective of this paper is to seek a more explicit understanding of these primary environmental determinants of biogeographic pattern and evolutionary process. In preceding sections, I have considered the separate influence of light, thermal and water regimes and their combined influence on growth regimes of the major response groups, designated megatherm, mesotherm, microtherm. Now, I propose to consider the patterns that result from overlap of these primary response groups and implications for taxonomic diversity.

Biogeographic regions

In a major phytogeographic analysis of Australia, Burbidge (1960) recognized three principal floristic zones (Tropical, Temperate, Eremaean) and three interzones based principally on climate, but also upon known distribution patterns of higher taxa of plants. She also recognized a basic division within the arid Eremean zone based upon the dominance of either summer or winter rain. Particular attention was devoted to a number of focal areas of high endemism and/or taxonomic diversity. These were northeast Queensland, the McPherson-Macleay overlap, Tasmania and southwestern Western Australia. Although boundary conditions were not quantitatively defined and the map scale large, Burbidge's map reflects her very considerable insight into patterns of plant distribution in relation to primary environmental controls.

Extending the analysis to include New Guinea, it is possible to closely match the Burbidge zonation and to provide additional insight into major floristic patterns by a simple overlay of the currently dominant megatherm and mesotherm patterns (Fig. 9). The difference lies in the fact that all boundaries shown were generated using defined functions and explicit procedures. The choice of mean growth index values is arbitrary (0.15, 0.30, 0.45), but these boundary conditions most closely match those used by Burbidge.

The most important difference to emerge from this comparison lie in the fact that there are four major zones of overlap of megatherm and mesotherm environments with relatively favourable conditions for growth (G.I. >0.45). By far the largest of these is the submontane zone of New Guinea, followed by northeast Queensland, the McPherson-Macleay overlap zone and a smaller zone in; central eastern Queensland. Each of these overlap zones is characterized by high taxonomic diversity and moderate to high endemicity of plant (and animal) taxa. Although not shown in Figure 9, because of scale limitations, much of western Tasmania is a zone of overlap of mesotherm and microtherm environments with relatively favourable conditions for growth of both elements (G.I. >0.45). The southwest of Western Australia is predominantly mesotherm; it is not a zone of significant overlap, but has a high level of plant taxonomic diversity and endemicity. The reason for this divergence from the general pattern must be sought elsewhere, in long isolation and divergence from a common inheritance of mesotherm stocks with southeastern Australia.

Taking this general problem of bioclimatic zonation one step further, data generated in the preceding analysis of environmental control of plant response have been used in a numerical taxonomic classification of bioclimate of Terra Australis. This is not the place for a detailed discussion of procedure, but suffice to say that the program MULCLAS in the CSIRO classificatory package TAXON was used. Of the alternative classificatory strategies available, that involving the Euclidean metric with group averaging was employed. A selected matrix of 500 stations in Terra Australis x 33 bioclimatic attributes formed the basis of the classification. For each of the three basic response groups, megatherm, mesotherm, microtherm, the set of attribute data used was: weekly mean G.I(*a*); highest weekly mean G.I(*b*); lowest weekly mean G.I(*c*); annual weekly range G.I., (i.e., *b-c*); seasonality of G.I., (i.e., *b-c/a*); mean G.I. spring (Sept.-Oct.-Nov.); mean G.I. summer (Dec.-Jan.-Feb.); mean G.I. autumn (March-April-May); mean G.I. winter (June-July-August).

In addition, the separate influence of the water regime was included with the attributes: weekly mean M.I; seasonality index (C.V.); mean M.I. spring; mean M.I. summer; mean M.I. autumn; mean M.I. winter.

The resultant bioclimatic zonation of Terra Australis is shown in Figure 10, but only the major divisions have been indicated. A primary division separates all New Guinea plus northern and northeastern Australia with a very narrow coastal strip extending southward into the extreme eastern tip of Victoria from the rest of continental Australia. This separation is based on presence/absence of significant plant response during the summer season. A secondary division isolates a zone of southwestern Western Australia plus southeastern Australia and Tasmania from the rest of continental Australia largely on presence/absence of significant plant response in the winter season. Thus, the first two divisions separate out a northern and eastern zone with significant summer plant response, a southern and eastern zone with significant winter plant response and a very large interior zone with limited plant response in either season. The classical Torresian, Bassian and Eyrean zones emerge, albeit with somewhat altered but explicitly defined boundaries.

The inclusion of New Guinea leads to further modification. A third-order boundary separates montane and sub-montane environments from lowland New Guinea or mesotherm combined with microtherm from megatherm environments. The mesotherm/microtherm zone corresponds with the Tumbunan zone of Schodde and Calaby (1972), and the classification does indicate some affinity with bioclimatic outliers in eastern and northeastern Australia. A lower order subdivision within the megatherm zone separates seasonal from non-seasonal environments. These in turn correspond with the classical Torresian and Irian zones of Schodde and Calaby (1972).

The classification highlights the very limited bioclimatic affinities of lands on either side of Torres Strait. Only a very small area of lowland coastal northeast Queensland (i.e. Tully-Gordonvale) is included with much of lowland New Guinea in the megatherm non-seasonal Irian zone. Even so, this small Australian enclave represents an attenuated and modified form of the megatherm non-seasonal environment and separates from New Guinea at lower levels in the classification. The megatherm seasonal environment (Torresian zone) is best developed in northern Australia with small outliers in southern New Guinea. A further subdivision shows that the most strongly seasonal, megatherm environments of northern Australia have no counterparts across Torres Strait in southern New Guinea, whilst the seasonal megatherm environments of the Trans-Fly area and the Port Moresby 'dry' strip have closest affinity with the eastern coastal strip of Cape York (i.e. Iron Range-McIlwraith Range), as shown by the broken line in Figure 10.

Within continental Australia, further subdivision separates out broad interzones between megatherm mesic and xeric environments and mesotherm mesic and xeric environments, leaving a residual core zone of xeric environments that correspond with the classical Eyrean or Eremaean zone. Thus, historical zonations based largely upon intuitive ordering of plant and animal distribution data are supported by a classification based upon explicit procedures and quantitative models of basic eco-physiological response of plants to major environmental regimes.

Summarizing the results of the numerical taxonomic analysis, five primary bioclimates and two major interzones can be distinguished and their approximate correspondence with existing biogeographic terminology can be indicated.

(1) Megatherm, non-seasonal	Irian
(2) Megatherm, seasonal	Torresian
(3) Mesotherm/microtherm, non-seasonal	Tumbunan
(4) Mesotherm/microtherm, seasonal	Bassian
(5) Megatherm/mesotherm, arid	Eyrean (Eremaean)

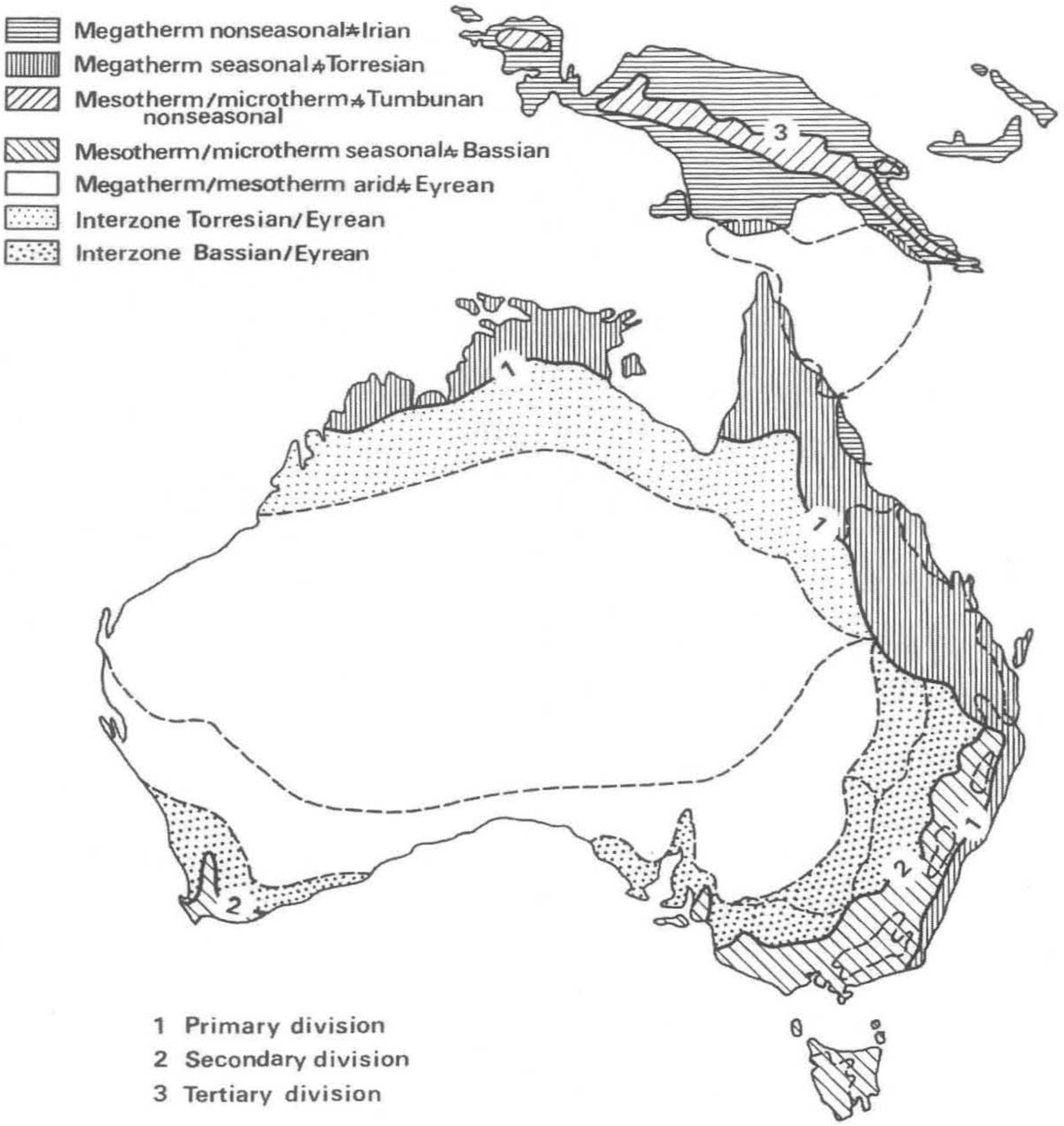

Megatherm nonseasonal≠Irian
Megatherm seasonal≠Torresian
Mesotherm/microtherm≠Tumbunan nonseasonal
Mesotherm/microtherm seasonal≠Bassian
Megatherm/mesotherm arid≠Eyrean
Interzone Torresian/Eyrean
Interzone Bassian/Eyrean
1
2
3
1 Primary division
2 Secondary division
3 Tertiary division

Fig. 10. Bioclimatic classification of Terra Australis.

The two major interzones are essentially semi-arid environments linking primary bioclimates (1) and (5) across northern Australia and primary bioclimates (4) and (5) across southern Australia.

Further examination of the patterns in Figure 10 will show that major geographic disjunctions occur between component bioclimatic regions. Thus, within the mesotherm/microtherm seasonal bioclimate (Bassian) there is a large core area in southeastern Australia with outliers in Tasmania, southwestern Western Australia and the Mt Lofty Ranges and Kangaroo Island in South Australia. Differentiation of flora and fauna within this bioclimatic region is most pronounced between southwestern and southeastern sectors. Tasmania is differentiated largely on the basis of more extensive microtherm environments. Although only moderately disjunct, the South Australian enclaves do exhibit some differentiation of biota. Further disjunct occurrences of this bioclimate occur on mountain tops and plateaux at increasing elevation northwards in eastern Australia, but lack of climatic data and scale of map preclude their inclusion in Figure 10. Some of these disjunct Bassian regions have been designated as biogeographic regions in their own right (Kikkawa & Pearse 1969; Horton 1973), but there is no consistency of treatment.

Major disjunctions between northern Australia and New

Guinea have already been described, but within the megatherm seasonal bioclimate (Torresian) there are disjunctions between Cape York and northwestern Australia. In turn there is a lower order disjunction between the Kimberley region and the 'Top End' of the Northern Territory and some lesser differentiation of biota has occurred. The most important feature of the arid core zone of continental Australia is that it is essentially continuous, at least with respect to bioclimate. Here, disjunctions are generated by terrain and soil patterns (Pianka 1969; and see Northcote & Wright, Williams, this volume).

Taxonomic diversity

Various measures of taxonomic diversity have been proposed, but that used here is the simplest, the total number of species present within a given large area. In Australia, knowledge of plant and animal distributions has reached the point where it is possible, using published maps, to estimate potential species densities within defined areas. A large number of hypotheses have been advanced as explanation for observed gradients in taxonomic diversity and most of these have been summarized and ably reviewed by Pianka (1966). While the physical environment is usually assumed to be an ultimate factor, biotic processes such as speciation, immigration, competition and extinction are often invoked as proximate factors.

Here, it is not possible to do more than examine environmental correlates of taxonomic diversity. The environment is described by variables derived from a plant response model coupled to climatic input data. Preliminary analyses indicated that two simple measures carried most information about the plant response environment.

(a) Weekly mean growth index for the relevant response group, i.e. megatherm, mesotherm, microtherm, or the group indicated as best adapted for the given location. This is a measure of potential site productivity as determined by climate.

(b) Seasonality of growth response for the relevant group, i.e. coefficient of variation around weekly mean growth index. This is one measure of environmental stability or the magnitude of within-year resource fluctuations. Year-to-year variation is frequently invoked as a measure of environmental predictability, but the necessary data were not available for inclusion in this analysis.

Using distribution data only from continental Australia, the potential species densities within a 10km radius of 30 climate stations, selected as representative of bioclimates identified by numerical taxonomic analysis (*cf*. Fig. 10) were estimated for a number of plant and animal taxa: *Eucalyptus*, *Banksia*, *Maireana*, all terrestrial birds, honeyeaters (Meliphagidae), blossom-feeding parrots, seed-eating parrots, fruit-eating pigeons, seed-eating pigeons, finches, bats, marsupials, rodents, lizards, snakes, turtles and frogs.

Using only the two terms, weekly mean growth index and seasonality of growth index, combined in linear and/or quadratic form in multiple regression equations, the percentage of variance in species density accounted for ranged from a low of 18.4% in *Eucalyptus* to a high of 90.1% in bats (Table 1). The relatively poor explanation of variance in the plant groups is due in part to gross smoothing of source data (available only in 1° grid cells) and non-linearity of species density response along the productivity gradient due to competitive exclusion. For example, at very high levels of weekly mean growth index *Eucalyptus* species are usually absent due to competition from closed-forest species. The use of a more complex trend surface lifted the percentage of variance accounted for in *Eucalyptus* from 18.4% to 49.6%; in *Banksia* from 24.6% to 40.3% and *Maireana* (bluebush) from 63.8% to 72%. In all cases, the productivity term contributed most, but addition of the seasonality term significantly improved the correlation.

In the vertebrate animal taxa that were analysed, species densities of bats, rodents, snakes, turtles, pigeons and finches show best correlations with megatherm indices, indicating either more recent invasions of northern Australia or long-established palaeotropical elements. The

Table 1. Environmental correlates of species densities for selected plant and animal taxa in Australia. (Figures indicate percentage of total variance accounted for by different environmental indices and functions, where L = linear, Q = quadratic)

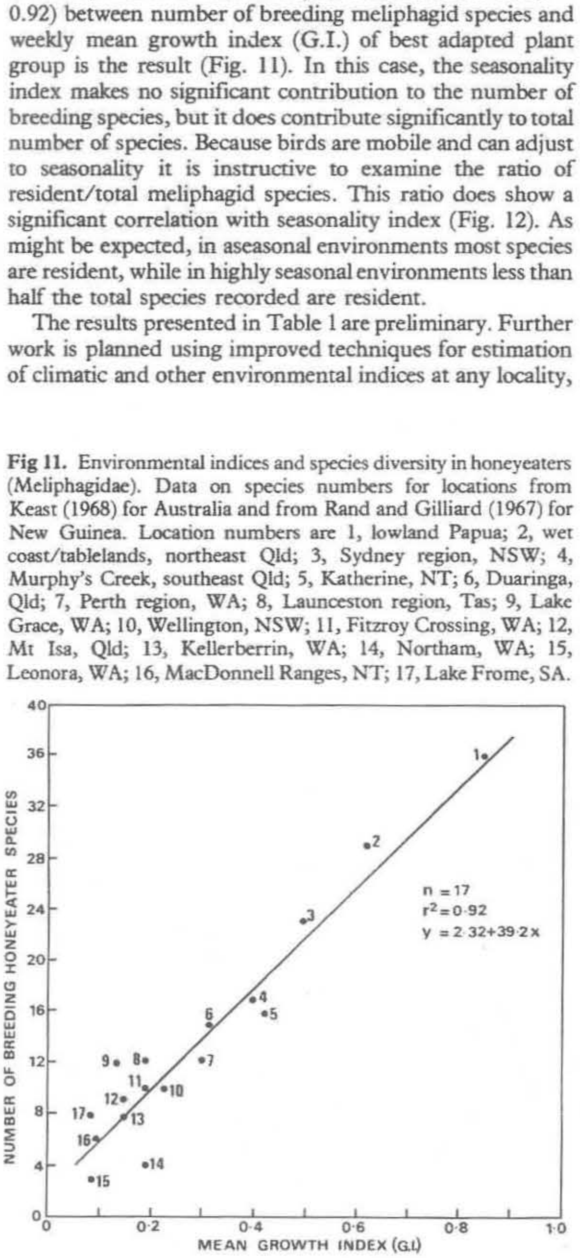
Degrees of freedom	Mesotherm G.I.		Megatherm G.I.		Best adapted G.I.		Moisture Index M.I.		Terrestrial birds	Honeyeaters (Meliphagidae)	Parrots (Frugivorous)	Parrots (Granivorous)	Pigeons (Frugivorous)	Pigeons (Granivorous)	Finches (Granivorous)	Bats	Rodents	Marsupials	Lizards	Snakes	Turtles	Frogs	*Eucalyptus*	*Banksia*	*Maireana*
	$\bar{x}$	C.V.	$\bar{x}$	C.V.	$\bar{x}$	C.V.	$\bar{x}$	C.V.																	
2	L	L							62.2	61.1	59.5	24.3	59.9	6.8	1.0	32.2	20.3	71.4	***60.9***	25.3	27.1	62.8	16.8	***24.6***	34.4
2			L	L					49.1	43.2	48.3	4.0	***81.5***	***28.4***	***63.2***	***90.1***	***52.9***	42.4	31.6	***72.1***	***66.1***	49.2	-4.4	3.4	36.0
2					L	L			***69.6***	***68.9***	***72.5***	***42.5***	75.1	19.1	39.1	67.0	42.6	71.3	58.0	43.8	49.0	***75.2***	12.9	13.8	***63.8***
2							L	L	65.5	64.5	65.9	13.1	68.6	10.4	13.0	45.6	19.7	***72.4***	56.4	34.3	41.2	71.4	***18.4***	19.4	60.5
2	Q	L							55.9	59.6	55.4	21.5	56.4	3.0	4.2	30.5	25.7	58.4	48.7	19.7	22.4	54.9	8.6	14.1	26.8
2			Q	L					41.1	29.5	35.2	2.6	71.0	***37.5***	***76.1***	41.7	35.0	31.2	***62.3***	***58.8***	39.1	-4.0	4.6	***25.2***	25.2
					Q	L			***63.4***	***62.2***	***67.0***	***45.0***	***75.3***	19.0	36.2	***64.5***	***44.7***	62.8	54.0	38.9	***43.5***	***67.7***	6.8	9.8	50.5
							Q	L	58.9	57.9	60.0	11.5	66.4	10.3	13.1	44.2	22.5	***63.9***	51.0	29.6	36.4	63.4	***10.0***	13.7	***54.9***
3	L+Q	L							61.9	60.2	58.5	34.5	59.1	11.8	3.9	31.0	24.4	73.7	***62.9***	25.2	25.7	62.4	29.8	***30.8***	33.8
			L+Q	L					49.4	50.9	52.6	2.0	***83.5***	***44.8***	***79.9***	***91.5***	***54.7***	44.4	30.1	***72.6***	***65.4***	51.3	-4.3	2.5	38.7
					L+Q	L			***70.4***	***69.5***	***72.3***	***53.1***	75.6	17.4	37.7	66.4	43.5	73.4	58.1	43.1	48.6	***76.2***	***38.6***	26.6	***68.9***
							L+Q	L	67.5	66.0	66.4	29.5	67.9	9.5	11.3	44.5	21.2	***75.8***	58.1	35.3	41.0	74.3	32.5	23.2	60.1
5	TREND								66.3	63.7	63.1	32.1	58.0	12.5	11.2	***91.8***	***22.2***	75.5	***62.9***	24.6	25.4	67.6	33.7	27.9	31.5
			TREND						54.9	56.5	54.5	9.7	***87.3***	***65.8***	***85.2***	91.5	***66.1***	51.7	32.2	***73.3***	***63.0***	53.1	-7.6	0.4	38.1
					TREND				70.8	71.5	74.5	***53.6***	76.7	47.7	57.3	71.9	55.7	76.0	57.4	47.0	58.1	***76.9***	***49.6***	***40.3***	***72.0***
							TREND		***73.5***	***72.6***	***69.7***	26.3	66.4	21.6	26.4	43.3	41.3	***76.9***	56.9	33.1	40.4	76.0	33.1	21.0	61.6

birds, marsupials and frogs show best correlations with the indicated best-adapted group, i.e. either megatherm or mesotherm, at a given location. This would suggest either long establishment and differentiation and radiation into the range of available environments or, in birds and marsupials, that homeothermy allows them to occupy diverse thermal environments.

Where the quality of distribution data is high in that it is possible to list the number of species directly observed within a relatively homogenous environment for which climatic data are available, correlations are markedly improved. For example, consider the number of breeding species of honeyeater (Meliphagidae) at 17 locations around Australia (Keast 1968) plus one lowland location in New Guinea (Rand & Gilliard 1967). An excellent linear fit ($r^2 = 0.92$) between number of breeding meliphagid species and weekly mean growth index (G.I.) of best adapted plant group is the result (Fig. 11). In this case, the seasonality index makes no significant contribution to the number of breeding species, but it does contribute significantly to total number of species. Because birds are mobile and can adjust to seasonality it is instructive to examine the ratio of resident/total meliphagid species. This ratio does show a significant correlation with seasonality index (Fig. 12). As might be expected, in aseasonal environments most species are resident, while in highly seasonal environments less than half the total species recorded are resident.

The results presented in Table 1 are preliminary. Further work is planned using improved techniques for estimation of climatic and other environmental indices at any locality, and location-specific data for species distribution. From the results obtained above it is clear that there is a powerful environmental determinism of taxonomic diversity, with the primary plant productivity term as the major component and seasonality of plant response as a secondary component. While there is a significant linear relationship between productivity and species density at lower levels of productivity in all groups examined, in many cases (e.g. more arid-adapted groups such as the seed-eating finches, pigeons and parrots, bluebush, *Banksia, Eucalyptus*), peak species numbers are achieved at an intermediate level of productivity followed by a sharp decline at higher levels. For instance peak numbers of *Eucalyptus* species occur at weekly mean G.I. values of 0.5-0.6. Presumably, this can be interpreted as the result of competitive exclusion by better-adapted mesic, closed-canopy species at higher levels of productivity. More precise specification of ecophysiological responses, distributions and site parameters should lead to more precise formulation of such relationships between environment and taxonomic diversity.

Fig 11. Environmental indices and species diversity in honeyeaters (Meliphagidae). Data on species numbers for locations from Keast (1968) for Australia and from Rand and Gilliard (1967) for New Guinea. Location numbers are 1, lowland Papua; 2, wet coast/tablelands, northeast Qld; 3, Sydney region, NSW; 4, Murphy's Creek, southeast Qld; 5, Katherine, NT; 6, Duaringa, Qld; 7, Perth region, WA; 8, Launceston region, Tas; 9, Lake Grace, WA; 10, Wellington, NSW; 11, Fitzroy Crossing, WA; 12, Mt Isa, Qld; 13, Kellerberrin, WA; 14, Northam, WA; 15, Leonora, WA; 16, MacDonnell Ranges, NT; 17, Lake Frome, SA.



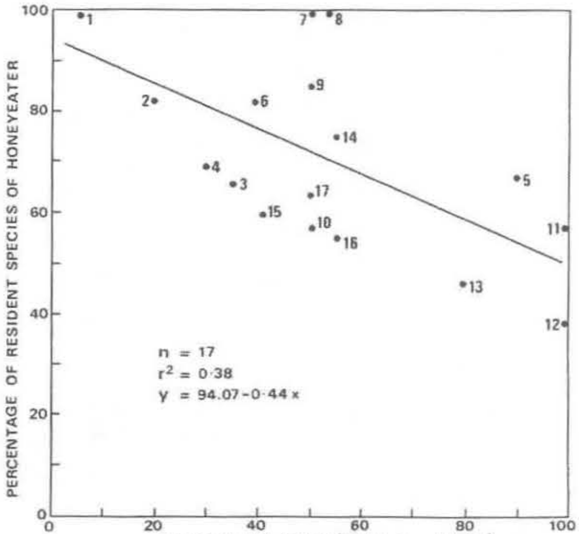


Fig. 12. Percentage of resident honeyeater species as a function of seasonality (coefficient of variation of weekly G.I.). Location numbers as for Figure 11.

Origins and evolution of the biota

As early as 1859 the eminent botanist J.D. Hooker identified four distinctive elements in the Australian flora: a cosmopolitan element; an autochthonous (Australian) element of mainly xeromorphic taxa; an Indo-Malayan element of mainly mesic, rainforest taxa; an Antarctic element of cool-temperate taxa typified by *Nothofagus*. By linking the last three groups with presumed areas of origin, Hooker set a precedent that has been followed right up to the present. Preoccupation with identification of centres of origin and source areas for the Australian biota has emphasized dispersal hypotheses. Essentially, these argue that Australia (and particularly New Guinea) received its biota through active dispersal or migration from centres of origin which, until recently, were deemed to be in the northern hemisphere. With the advent of plate tectonic theory it is allowed that significant elements of the biota entered via a southern route late in the Cretaceous and in the early Tertiary (Raven & Axelrod 1972). But, emphasis remains on dispersal, migration and invasion of organisms from source areas on other land masses. This viewpoint is exemplified in the works of Simpson (1940, 1952, 1961), Mayr (1940, 1944, 1962), Darlington (1949, 1956, 1965) and Keast (1961, 1973).

An alternative, vicariance hypothesis argues that the Australian biota evolved *in situ* through fragmentation of ancestral stocks present on Gondwanaland in the mid to late Mesozoic and their subsequent differentiation in isolation. Disjunct distributions of plant and animal taxa are seen primarily as evidence of shared ancestry in the distant past, rather than as evidence of dispersal from some putative centre of origin. The reality of over-water dispersal of many organisms is not denied, but its significance for evolution of continental biotas is minimized. This competing paradigm is exemplified in the works of Croizat (1952, 1958, 1964) and supporters (Croizat *et al.* 1974). While there is good evidence for limited and more recent (post-Miocene) additions to the Australian biota by dispersal from the north (e.g. rodents), there is mounting evidence to suggest that the vicariance hypothesis most satisfactorily explains the broad foundations of the Australian biota.

In order to assess the environmental changes and possible evolutionary pathways for the biota of Terra Australis it is necessary to revert to terminology developed earlier in this paper. Firstly, in terms of the thermal adaptation of the flora (and associated fauna) three broad groups are recognized, megatherm, mesotherm, microtherm. Commonly, these physiological response groups have been labelled with terms implying ultimate origins, megatherm being described as Indo-Malayan, Malesian or Tropical, mesotherm as Autochthonous or Australian, and microtherm as Antarctic. However, evidence will be presented that environments favourable for each of the major thermal response groups persisted on the developing land mass of Terra Australis throughout the past 150 million years and the whole period of evolution of the higher plants and animals. Fossil evidence for the presence of important members of the microtherm and mesotherm flora is unequivocal and predates the separation of Australia from Antarctica. Lack of fossil evidence from northern Australia precludes a firm statement about the megatherm element, but prominence of palaeotropic elements suggests early isolation from common Gondwanan stocks.

While uncertainties remain with respect to palaeolatitudes of Gondwanan land masses, there seems little doubt that Antarctica has remained close to the South Pole throughout the later Mesozoic and entire Tertiary periods. Using the most recent available syntheses of timing and motion of component land masses (Crook 1981; Powell *et al.* 1981), the broad latitudinal limits of Terra Australis, Antarctica and Greater India have been estimated through the past 150 million years (Fig. 13). Superimposed on this framework are shown the position and dating of sea-surface palaeotemperatures that have been used in progressive adjustment of equator-pole sea-surface temperature gradients through time. These temperatures then provide the basis for estimating the potential distribution and extent of the three primary plant response groups and their overlap patterns. The criteria used were the same as for Figure 2, and are no more than approximations based on annual mean air temperatures.

megatherm dominant = mean air temperature $> 24°C$
megatherm/mesotherm = mean air temperature $> 20°C < 24°C$
mesotherm dominant = mean air temperature $> 14°C < 24°C$
mesotherm/microtherm = mean air temperature $> 12°C < 14°C$
microtherm dominant = mean air temperature $< 12°C$

Obviously the patterns of spatial and temporal change shown in Figure 13 are highly generalized and reflect thermal environments at or close to sea-level. The additional influence of uplift and mountain building becomes progressively more important with passage through the Tertiary period. Development of the eastern highlands of Australia and the high central cordillera of New Guinea provided extension of favourable mesotherm and microtherm environments northwards into low latitudes. Superimposed on the general global cooling trend throughout the Tertiary are the extreme temperature oscillations of the glacial-interglacial cycles of the Quaternary, but these can not be shown at the scale used in Figure 13. The major point to be made from this analysis is that extensive areas with thermal environments favourable for each of the megatherm, mesotherm and microtherm elements have persisted on the evolving land mass of Terra Australis throughout the past 150 million years. The extensive radiations of plant and animal groups and patterns of speciation in Terra Australis must have a far greater time depth than is currently accepted.

The rifting of Greater India from East Gondwana in the early Cretaceous had no apparent significant effect on global climate. Before rifting and separation, much of Greater India lay within a megatherm-dominant environment and remained within it as it rafted northwards across the equator. Uplift and mountain building probably preserved some mesotherm environments, but the apparent absence of 'typical' Gondwanan angiosperms in the fossil record of India should not be surprising, since these are mainly mesotherm and microtherm elements. A similar argument applies to Africa, but mesotherm environments did persist in southern Africa and on Madagascar. South America on the other hand retained extensive areas of both mesotherm and microtherm environments, as did Australia and New Zealand. The closer floristic affinities of these latter land masses are usually attributed to opportunities for later dispersal across land connections through Antarctica (Raven & Axelrod 1972). It is much more likely that persistence of mesic mesotherm and microtherm environments on all three land masses has permitted continued existence of conservative, slowly evolving stocks that shared a common inheritance in the Gondwanan land mass.

A gradual northward rotation of Australia/Antarctica commenced in the mid Cretaceous, but significant changes in global climate were not initiated until rifting and separation of Australia and Antarctica in the early Tertiary (Kemp 1978). The steady northward drift of Australia largely compensated for global cooling through the Tertiary and allowed persistence of extensive areas of thermal environments favourable for each of the major megatherm, mesotherm and microtherm elements. In fact, throughout the Tertiary, the broad thermal zonation across Australia remained relatively stable until the extreme oscillations of

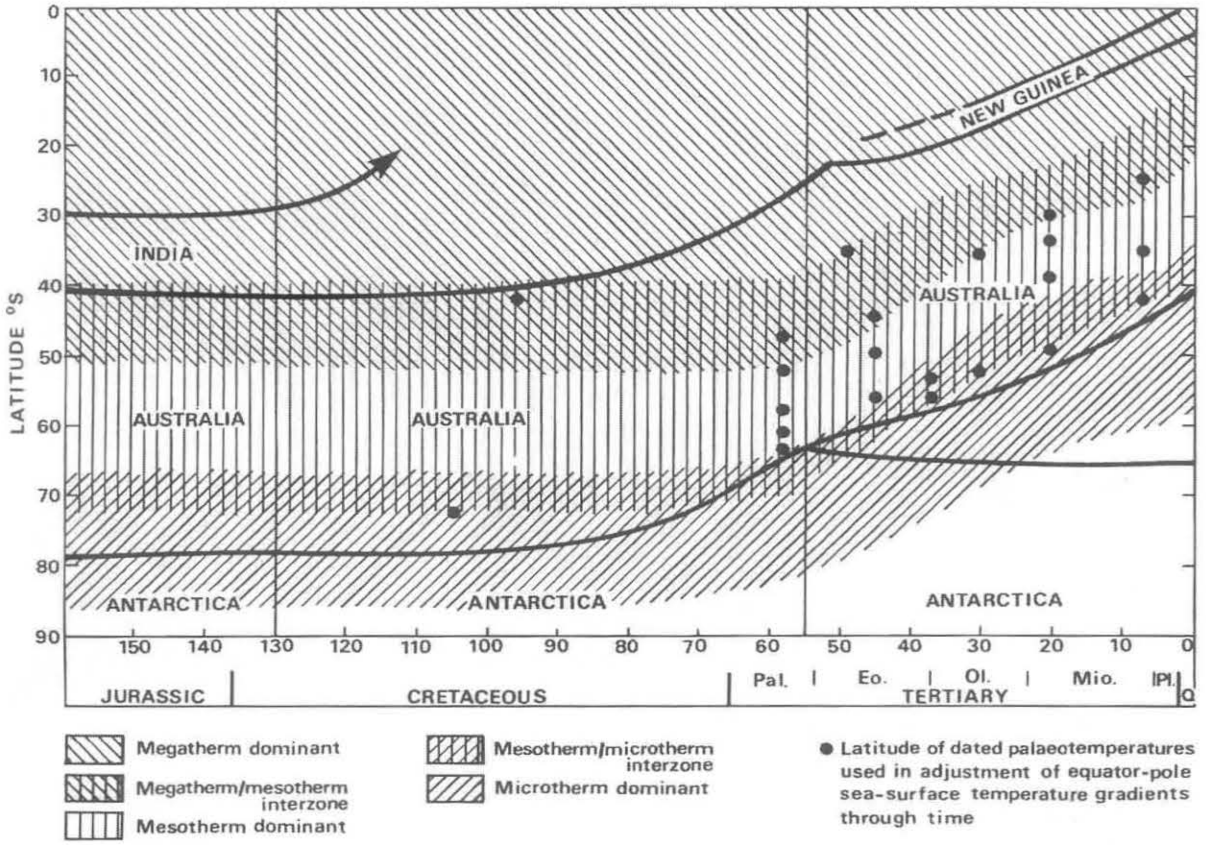


Fig. 13. Inferred consequences of continental movements and global climatic change on the distribution of primary thermal response groups in East Gondwana, Aust-Antarctica, Australia-New Guinea and Antarctica.

the past two to three million years. Microtherm dominant environments persisted on Antarctica throughout the Cretaceous and up until the Miocene, with a possibility of a mesotherm/microtherm overlap zone on the northernmost edge of Antarctica only in the Paleocene and early Eocene (Fig. 13).

This interpretation of events is at variance with prevailing views of Tertiary floras and inferred environments, particularly for southern Australia. Much has been made of the presumed 'tropical' affinities of the early Tertiary flora of southern Australia since widely-distributed fossil taxa have modern representatives confined to the geographic tropics (northeastern Australia, New Guinea, New Caledonia). Although much of this evidence is derived from pollen analysis, more recent research on macrofossil assemblages (Christophel 1981) appears to provide additional support for such, an interpretation.

Firstly, consider the fossil record based on pollen analysis. Identification of fossil taxa rarely extends beyond the generic level and often no further than sub-family or family level. At this level of classification a wide ecological adaptation and environmental tolerance is normally represented. If uniformitarian assumptions are adopted, i.e. patterns of genotype/environment interactions observed at present are held to have applied in the past, then careful analysis reveals that most of the presumed 'tropical' taxa are found today at relatively high elevations in the tropics and are dominantly mesotherm and even microtherm in response rather than megatherm. For example, a widely cited genus, *Anacolosa*, now confined to the tropics, does have a few species occurring in lowland megatherm environments, but most species are characteristic of mesotherm environments at higher elevations. A similar argument applies to modern representatives of the Cunoniaceae, another frequently cited 'tropical' or 'subtropical' group that is basically mesotherm in response.

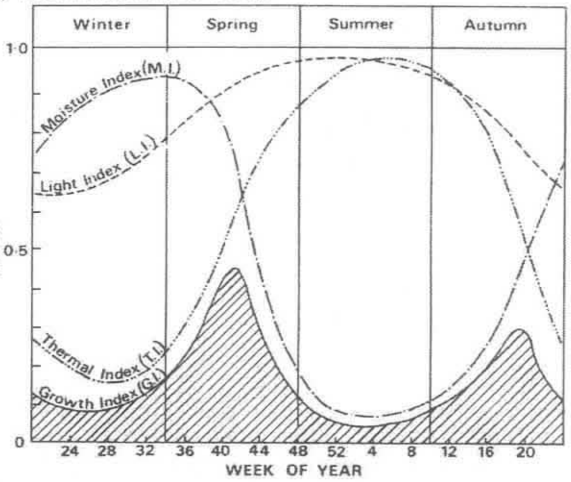
Secondly, consider the macrofossil assemblages analysed by Christophel (1981). Physiognomic analysis based on leaf size and shape for samples from early Tertiary deposits at three locations in southeastern Australia (Maslin Bay, South Australia; Anglesea, Victoria; Nerriga, New South Wales) revealed closest affinities with extant complex notophyll vine forest (NVF) and simple notophyll vine forest (SNVF) as defined by Webb (1959). This has been interpreted to reflect 'tropical/sub-tropical' conditions. However, both NVF and SNVF types today are dominant in mesotherm environments (*cf.* Fig. 4). Estimation of annual mean air temperature (using an algorithm based on latitude, longitude, elevation and 1/precipitation) for closed-forest sites used by Webb (1959) resulted in values of mean air temperature of 18.8±2.0°C for NVF and 18.6±3.3°C for SNVF. These temperatures very clearly fall within the mesotherm response category. Taking these temperature limits, annual mean temperatures across southern Australia during the early Tertiary need have been no more than 2-4°C warmer than at present to accommodate the fossil evidence.

Further clarification is needed on another aspect of past thermal environments. Much has been made of an apparent anomaly in season of growth response of some elements of the heath flora in southern Australia (Specht & Rayson 1957). Indeed, it has been suggested (Specht 1981) that major species of the upper stratum of southern Australian plant formations have retained a temperature response which evolved during the 'sub-tropical' Tertiary and that observed summer growth response is out of phase with the present winter-rainfall dominant environment. These elements then are considered to be relictual.

However, estimation of seasonal trends in light, thermal, moisture and growth indices using weekly mean climatic data for the type location, Keith, South Australia, indicates that observed responses are completely in accord with that of the expected mesotherm element and that no such anomaly exists. Depending on depth of root system and the extent of soil-water storage in the deep sand profile, the cut-off in growth response due to water stress will occur progressively later from late-winter through spring and into summer (Fig. 14). Optimum temperatures for the mesotherm response class at Keith are, very clearly, in summer. Sensitivity analysis indicates that maximum dry matter production in this environment should be obtained from a deep-rooted perennial with mesotherm response pattern. On shallow and otherwise edaphically dry sites, short-season annuals with a microtherm response pattern make best use of environmental resources. No growth strategy involving a megatherm response pattern can compete with either of these two alternatives.

Against this broad background of thermally adapted groups it now becomes necessary to superimpose changes brought about by increasing seasonality of both thermal and water regimes. These two components of seasonality tend to be linked, since onset of dry conditions with reduced cloud cover and clear skies is associated with wider diurnal and seasonal temperature ranges. While fossil evidence is biased towards wetter environments, available data suggest that mesic conditions prevailed over much of the southern two-thirds of Australia (as yet, no fossil evidence is available for the northern third of the continent) until the mid to late Miocene when evidence for drier conditions becomes available (Kemp 1978). However, evidence for lateritic deep weathering in the Paleocene suggests that some seasonality of water regime existed even at that time. While plants growing on deep soils may not have experienced seasonal water stress, this would not be the case for plants growing on edaphically dry sites, e.g. skeletal, rocky soils or coarse dune sands. The evolution of scleromorphic features, so characteristic of much of present day Australian vegetation, could have been initiated in such edaphically dry sites in otherwise mesic environments as far back as the early Tertiary or even the late Cretaceous, 60-70 million years ago. Progressive adaptation to these more xeric sites may have been facilitated by adaptation to conditions of gross mineral nutrient deficiency in deeply weathered soils and deep sands derived from coarser-textured sediments (Andrews 1914; Beadle 1954, 1966).

(a) 100 mm available water storage



(b) 250 mm available water storage

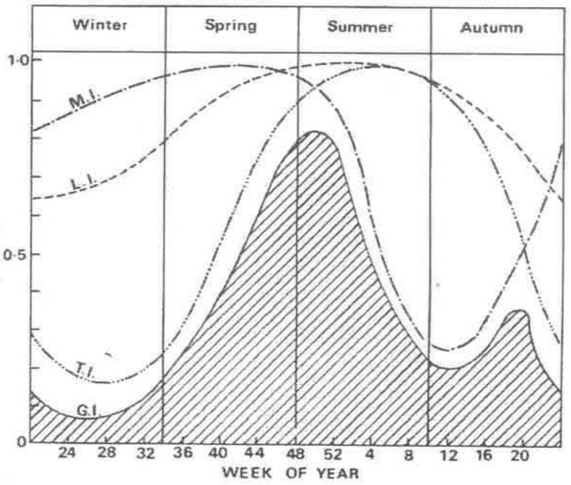


Fig. 14. Pattern of indicated responses for a mesotherm plant growing at Keith, South Australia, with **a**, average (100mm) and **b**, high (250mm) available water storage in the root zone.

While much attention has been focused on the role of increasing aridity in the progressive adaptation of flora and fauna and radiation into more xeric environments in Australia, I believe that increasing seasonality of both thermal and water regimes throughout the Tertiary has been the primary factor in evolution of the Australian biota. Although mean air temperatures indicate continued persistence of environments favouring all three thermal response groups on the evolving land mass of Terra Australis (Fig. 13), increasing seasonality of thermal regimes would promote ecological sifting and adaptation, and differential extinction because temperature extremes (particularly minimum temperatures) would exceed lethal limits of some component elements. Again, while mean moisture regimes might appear to be generally favourable, the occurrence of regular seasonal water deficits, even of short duration, exerts a powerful influence on ecological segregation of biotic elements. The general pattern of climatic change through the Tertiary has been one of increasing duration of periods with water deficit and increase in the area so affected. The present arid and semi-arid climates of Terra Australis represent points along a continuum of increasing duration of periods of water deficit. Available evidence indicates that significant expansion of areas with water regimes at the drier end of this continuum commenced in the Miocene (Kemp 1978).

A test of the hypothesis that increasing seasonality has been a primary factor in the ecological sifting and differentiation of basic ancestral stocks inherited from Gondwana is to examine the distribution and relative abundance of presumed older, more generalized and least specialized biotic elements in relation to measures of seasonality. Firstly, at a qualitative level (*cf.* Keast 1981), both plant and animal taxa that appear to remain closest to ancestral stocks are concentrated in mesic aseasonal near-isothermal environments, whether these be megatherm, mesotherm or microtherm. This can be interpreted to mean that these old conservative elements of the biota survive relatively unchanged in those environments that have persisted with least change since the later Mesozoic and early Tertiary.

Data provided by Specht *et al.* (1974) for the numbers of seed plant genera retaining primitive characteristics in different regions in Australia permit a more quantitative analysis. Various measures of seasonality were estimated for each region, including seasonality of water regime (*cf.* Fig. 5), seasonality of thermal regime for each of the megatherm, mesotherm and microtherm elements, seasonality of growth response (coefficient of variation of weekly mean growth index) for each element, and seasonality of growth response for that element best adapted to a particular region. This last measure proved superior and gave a highly significant linear relationship ($r^2 = 0.75$), with the number of 'primitive' seed plant genera inversely related to degree of seasonality (Fig. 15). This general relationship holds whether seasonality of growth conditions be induced primarily by temperature, as in Tasmania, by moisture regime, as in northwestern Australia, or by a combination of both, as in New England.

Taxonomic diversity at species level would seem to be a function of both environmental productivity and seasonality (Table 1). But, at this level, those species exhibiting more primitive characteristics also demonstrate an inverse relationship between number of such species and seasonality index (Fig. 16). The subregions within southwestern Australia plotted separately yield a particularly good fit ($n = 6$; $r^2 = 0.99$) but with a near doubling of species numbers at a given level of seasonality compared with other regions of the continent. This would appear to be due to extensive radiation within genera retaining primitive characteristics (particularly within the Proteaceae). Lest this be thought to be a phenomenon associated solely with the presumed long isolation of southwestern Australia, inclusion of data from the Central Coast and Central Tableland regions of New South Wales indicates that the rich sandstone flora (also rich in proteaceous species) of the east conforms with the steeper relationship ($n = 8$; $r^2 = 0.79$). The two relationships may be indicative of sandstone/sandplain flora versus the rest rather than of an exclusively southwestern phenomenon. In summary then, the more 'primitive', 'relict' and older endemic elements of the flora (and associated fauna) are concentrated in regions of reduced seasonality, whether this be induced by thermal or moisture regimes or both.

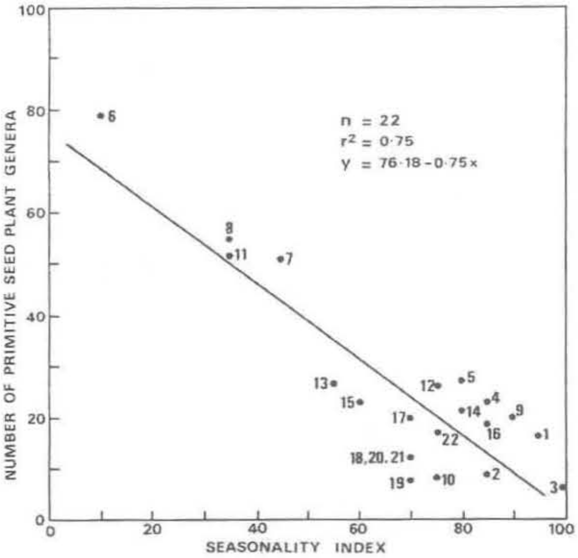
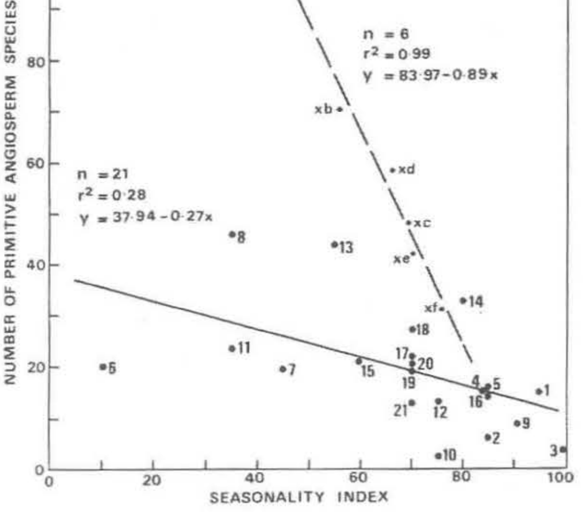


Fig. 15. Primitive Australian seed plant genera (after Specht *et al.* 1974) as a function of seasonality of growth conditions (coefficent of variation of weekly mean growth index). Floristic regions are 1, Kimberley, WA; 2, Central Australia, NT; 3, Semi-arid NT; 4, 'Top End', NT; 5, Cape York, Qld; 6, Wet Coast/Tablelands, north Qld; 7, East central Qld; 8, Southeast Qld; 9, Northwest Qld; 10, Southwest Qld; 11, North Coast, NSW; 12, Northern Tablelands, NSW; 13, Central Coast, NSW; 14, Central Tablelands, NSW; 15, South Coast, NSW; 16, Southern Tablelands, NSW; 17, Northeast Vic; 18, Southwest Vic; 19, Mallee, Vic; 20, Southeast SA; 21, Eyre Peninsula, SA; 22, Southwest WA.

Fig. 16. Australian angiosperm species retaining primitive characters (after Specht *et al.* 1974) as a function of seasonality of growth conditions. Districts of southwest Western Australia are plotted separately: a, Stirling; b, Darling; c, Avon; d, Eyre; e, Warren; f, Irwin. Other floristic regions are numbered as in Figure 15.



One final point concerns the long-standing and understandable preoccupation with the massive climatic oscillations of the Quaternary as a powerful agent in evolution of the biota of Terra Australis. It is difficult not to be impressed with the evidence for substantial adjustments in the latitudinal and altitudinal range of primary climatic environments and associated organisms. It is tempting to look for explanations for observed patterns of taxonomic diversity in terms of these past oscillations rather than in terms of present day environment. While not denying the influence of the past, the view developed in this paper is a strongly deterministic one; present day distributions reflect present day environments! Only by developing a thorough understanding of organism/environment interactions in the present are we likely to be able to interpret the influence of past environment on pathways of evolution.

A general conclusion to emerge from the present analysis is that major radiation and differentatiation of the biota took place long before the Quaternary and indeed, for many groups, far back in the Tertiary. Even at the level of speciation, the Quaternary climatic fluctuations may ultimately prove to have had no more than a 'cosmetic' effect upon already existing taxa and their major influence may have been one of differential extinction. If supported, these views would suggest a diminution of the role of 'refuge area'-based allopatric speciation, and potentially greater importance of parapatric modes of speciation.

It is important to recognize that present day climate and vegetation patterns are, in a sense, anomalous with respect to prevailing longer-term patterns. Present climate is representative of short-term warm 'spikes' of 5-10,000 years that recur at relatively long intervals of 80-120,000 years. Equally anomalous are the short-term cold 'troughs' of full glacial conditions, encompassing 5-10,000 years, that recur at similar long-term intervals. For much of Quaternary time, climatic conditions fluctuate between these extremes with generally lower temperatures and, for many regions, more effective water regimes than at present. Thus, for Terra Australis, climatic conditions and vegetation patterns would more nearly approach those continued on from the later Tertiary. The major effect of the most recent cold arid phase, which occurred 15-20,000 years ago and was perhaps amplified by the presence of aboriginal man and his tool of fire, has been extinction of large numbers of plant and animal species that had survived all previous climatic perturbations.

Given these fluctuations of global climate throughout the recurring glacial-interglacial cycle, favourable environments for any given taxon will expand and contract and, at least locally, disappear. The unique and localized environments of today may be dominant in the next phase of global climate. We need to identify, locate and conserve such refugia and their component biota because the rare, relict and disjunct populations of today may be the source of the biotic patterns of tomorrow.

Concluding remarks

In this paper I have sought for a more explicit understanding of environmental determinants of biogeographic pattern and evolutionary process. Climate, interacting with terrain and soil to produce distinctive radiation, temperature, moisture and nutrient regimes, is seen as the primary determinant of pattern and process. The use of a generalized plant response model coupled to an extensive climatic data base for Terra Australis has provided a more relevant description and specification of environmental domains. I hope that the continental scale analysis and synthesis will provide a framework within which evolution and adaptation of organisms in the arid zone may be assessed.

Although dominated by the fact of severely limiting water regimes, the arid zone as currently recognized is but one end of a continuum. Only very limited areas of Australia have less than three months of each year with severe water deficits (Fig. 4). In terms of seasonality of the water regime, much of the arid zone is only moderately seasonal (Fig. 5) and has a probability, albeit low, of rainfall in both summer and winter seasons. This factor distinguishes the Australian arid zone from other major mid-latitude deserts where water regimes are highly seasonal.

Recognition of broad plant groups with characteristic temperature response patterns obviates the confusion in the literature associated with terms such as tropical, subtropical and temperate, that have geographic as well as thermal connotations. The arid zone currently is dominated by megatherm response groups in the north and mesotherm response groups in the south, with a wide zone of overlap in the middle. In colder arid glacial times a microtherm response element must have been prominent.

Available data suggest that extensive areas with environments favouring each of the megatherm, mesotherm and microtherm elements have persisted on the developing land masses of Terra Australis for at least the past 100 million years and possibly for 150 million years, that is throughout the whole period of evolution of the higher plants and animals. Rafting northwards of the Australian plate has compensated for the general global cooling in the Tertiary. However, the steepening of the equator-pole temperature gradient led to strengthening of the mid-latitude high pressure systems and of global winds and ocean currents. The net effect has been an increase in seasonality of both thermal and water regimes. This departure from the much more stable thermal and water conditions of the later Cretaceous and early Tertiary is postulated to be a major agent of evolutionary change, exceeding in importance the general increase in aridity in the later Tertiary and the extreme climatic fluctuations of the Quaternary.

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